The Role of Invertebrates in the Decomposer System

By J. B. CRAGG[1]

Every ecosystem has an association of organisms which, combined with abiotic environmental factors, brings about the destruction and simplification of the remnants of organic matter. This decomposer component, therefore, contributes to the recirculation of at least part of the chemical materials on which the functioning of the ecosystem depends.

The amount of material that passes into the decomposer segment of an ecosystem consists of a large part of the total primary production. In an uncropped ecosystem, everything finally enters the decomposer system. Even in systems that are cropped, a considerable part of the primary production is lost to man. Macfadyen (42) points out that in a grassland ecosystem used for raising cattle, some four-sevenths of the energy converted into primary production ends up as dead vegetation to be acted upon by decomposer organisms. The same general condition applies to woodlands. Ovington (53) has produced an energy budget for *Pinus* (pine) plantations in England which demonstrates that, over the 18-year period (17-35 years after planting), one-third of the net primary production is accumulated in the living trees, another third passes into the decomposer cycle, and only one-sixth is harvested by man. The relative proportions of the energy budget that ended up, over a 55-year period, in the different components of the ecosystem are shown in Figure 1.

No adequate estimates are available of litter production for coniferous forests in the Northern Rockies. Bray and Gorham (10) list only three areas in their arctic-alpine group: stands at 3000 meters in the Sierra Nevada, California, at 800 meters in southern Norway, and in the Kola Peninsula, USSR. The more extensive data for evergreen forest in the cool-temperate zone indicates an average total tree production of 13.2 metric tons per hectare per annum, of which three to four metric tons will be litter. Therefore, a litter fall of some one to three tons per annum can be expected to enter the decomposer system, along with root material, in many parts of the Northern Rockies.

There are no comprehensive accounts of the types, numbers, and activities of litter and soil invertebrates in Rocky Mountain ecosystems. However, certain generalizations are emerging from

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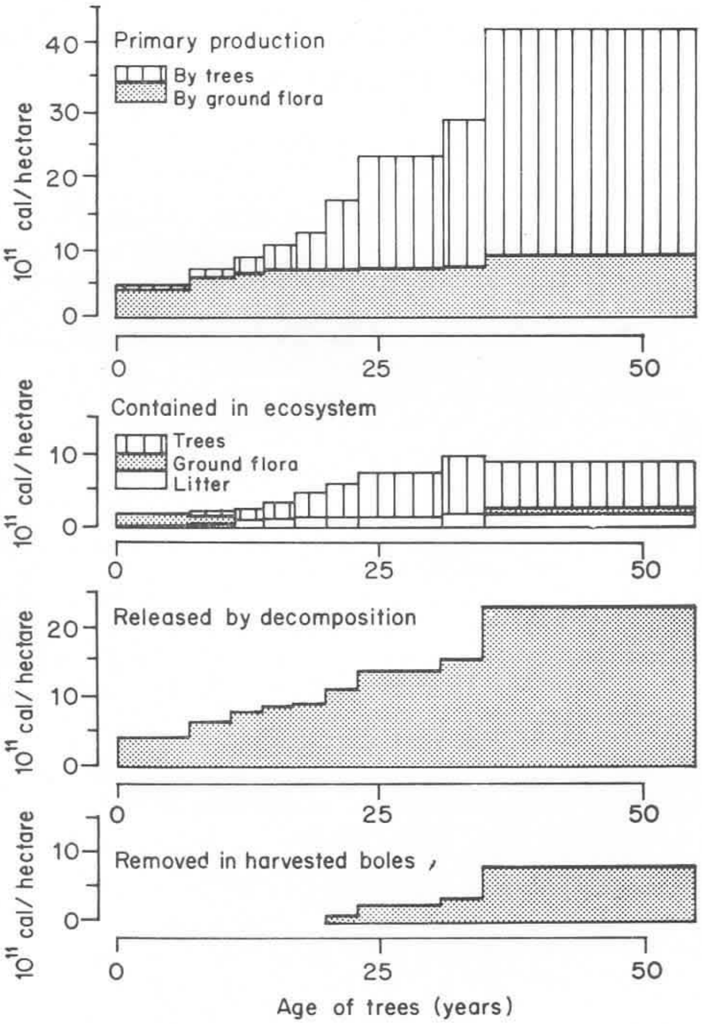


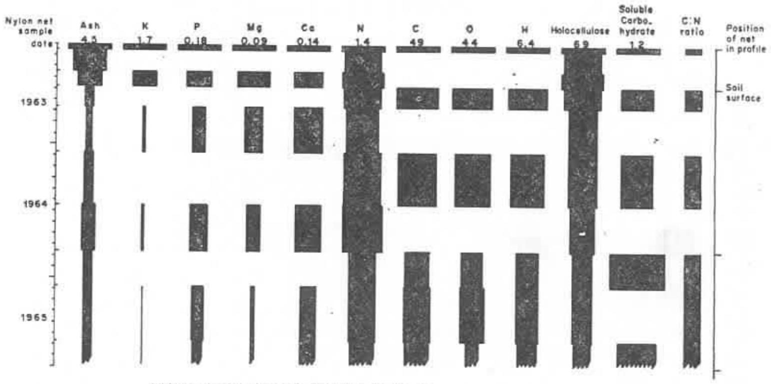
FIGURE 1. Energy budget for plantations of Pinus sylvestris **from time of planting (53).**

studies elsewhere, particularly studies in the cool-temperate regions of Europe. I shall describe these, in order to demonstrate the modern approach to studies on the decomposer system, hoping that they will provide the stimulus for much needed studies in the Rockies. The following major works give an up-to-date introduction to the literature and to the various points of view which characterize modern studies in soil biology: Doeksen and van der Drift (17), Burges and Raw (12), and Graff and Satchell (22).

Stages in the Decomposer System

Much of the material that falls to the forest floor will be attacked by a variety of organisms before it reaches the litter layer. Some of it will be converted into the faeces of both vertebrates and invertebrates, and considerable amounts will be invaded by elements of the microflora. As yet, we do not know how much decomposition takes place in the "above-ground" stage. Apart from the actual destruction of organic materials, other steps take place in the recycling of chemical substances, which short-circuit the main vegetation layer of a forest. Precipitation may remove both organic and inorganic constituents from the leaves. Carlisle, Brown, and White (13), for example, have shown that of the total amounts present in the litter layer of a deciduous woodland, 3 percent of the phosphorus, 72 percent of the potassium, and 70 percent of the nitrogen actually had been transported from the tree canopy by precipitation. In addition, they found that almost 90 kilograms per hectare of carbohydrate had been washed out of the "above-ground" parts of the trees. Some of this soluble material may have originated in the secretions of insects. Whatever its origin, it provides, on the leaf surface and in the litter, a nutrient source for some of the microflora.

The intensity of the decomposer processes is measured by the length of time required for decomposition to take place. Kendrick (33) has shown that it takes some nine years for needles of *Pinus*



RESULTS EXPRESSED AS % OF INITIAL CONTENT.
ASH AND INORGANIC CONSTITUENTS AS % OVEN DRY WEIGHT.
ORGANIC CONSTITUENTS AS % ORGANIC MATTER.

FIGURE 2. Chemical changes during decomposition of Juncus leaves in nylon nets. (38).

sylvestris (Scotch pine), when placed on the litter layer, to lose their characteristic form.

Kendrick and Burges (34) describe the succession of microfungi on such needles and provide information on the occurrence of some of the microfauna. Hayes (23, 24) has also followed the succession of microfungi on *Pinus sylvestris*; he has found some 120 species as against the 70 species recorded by Kendrick and Burges.

The results obtained by Latter and Cragg (38), although not concerned with coniferous litter, are relevant here. They studied

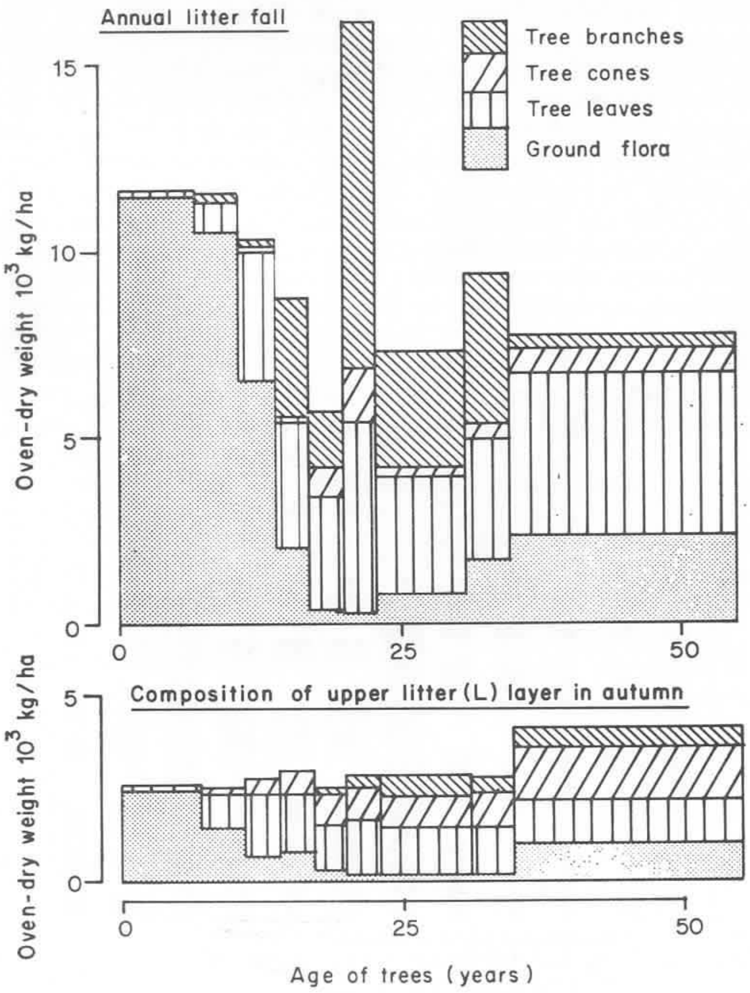


FIGURE 3. Litter fall and composition of surface litter in plantations of Pinus sylvestris **(53).**

the decomposition of leaves of the rush *Juncus squarrosus*, growing on redistributed acid peat in the cold, wet conditions of the northern Pennines in England. The site is similar in many ways to that of coniferous-bearing soils. The movement of leaves and leaf remnants down the profile, along with the accompanying changes in chemical composition and bacterial and fungal succession, were followed in detail for two and a half years, during which time the leaves retained their distinctive form. At the end of that period they had lost some 50 percent of their original dry weight and had reached the F_2 horizon some three to four centimeters below the surface of the litter. Figure 2 demonstrates the relatively slow rate of change in the major chemical constituents of *Juncus* (wiregrass) leaves during their passage into the F_1 horizon.

The rate of decomposition as shown by Shanks and Olson (59) depends upon temperature and altitude. Douglas and Tedrow (18), working with bog and tundra organic matter in the Arctic, recorded an annual decomposition rate of 2.8 percent dry weight loss. We can expect to find values of this order in much of the Northern Rocky Mountain area.

An important aspect of the decomposer cycle that has yet to receive adequate attention is the changing composition of the litter layer, both seasonally and on a long-term basis. Figure 3 shows these changes for *Pinus* (pine) plantations in England. Elements of the ground flora dominated the litter in the early years, and the more solid portions, e.g., cones, gradually increased with the increasing age of the stands. The different invertebrate communities associated with these different types of litter have not yet been studied in a quantitative manner.

The Invertebrates of Litter and Soil

In 1881, Darwin (15) clearly established that earthworms played a part in soil formation. Muller (44), in publications coincident with those of Darwin, described the role of soil invertebrates in general. Their publications, however, came too late to influence the development of soil science. That subject was already established as a branch of chemistry, as a result of the dramatic increases in crop production which followed the discoveries made by Liebig and by Lawes and Gilbert. Apart from some important taxonomic studies on individual groups of organisms, soil invertebrates and in particular their functions were almost completely neglected until Bornebusch (8) made a quantitative study of soil animals associated with Danish woodlands. He provided the first assessment of the metabolic function of soil organisms in the decomposition of forest litter. The publications of Jacot (28, 29, 30) presented a synoptic picture of the functions of soil animals in general, and his work is of special importance to us because it is largely concerned with studies in eastern North America.

An indication of the role of soil invertebrates in the decomposition and disappearance of leaf litter has been obtained by enclosing different types of litter in nylon nets of different mesh sizes and measuring the rate at which such material disappears. Bocock and Gilbert (6) and Bocock et al. (7), using this technique, showed that the rate of breakdown depended on the plant species, the chemical composition of the leaves, the local climate, and the type of soil fauna and flora. Edwards and Heath (19) used a modification of this technique in studying the breakdown of discs cut from leaves of deciduous woodland species. Their results show that the rate of breakdown depends upon whether or not soil invertebrates gain access to the leaves. Leaves contained in fine meshes that excluded almost all small invertebrates showed no decay even after nine months, by which time all, or at least the greater part, of the leaves in the larger mesh nets had been fragmented.

Fungi and bacteria may be present on plant material before it reaches the ground, where it is invaded by other species and is attacked by the litter-inhabiting invertebrates. The major animal groups associated with the decomposition of organic materials include Protozoa, Nematoda, Enchytraeidae, Lumbricidae, Gastropoda, and many orders of Insecta, of which the Collembola, Orthoptera, Isoptera, Hemiptera, Lepidoptera, Coleoptera, Hymenoptera, and Diptera may be represented by several hundreds of species. The Acarina and Myriapoda are other arthropods that play an important part in decomposition, particularly in coniferous forest soils. Kuhnelt (37) provides a broad account of the types and possible functions of organisms present in litter and soil.

The Protozoa, Nematoda, Enchytraeidae, Collembola and Acarina are universally present in coniferous forest soils, and all of them, apart from the Protozoa, have received detailed study. Very little study has been made of Formicidae, very often present in large numbers in coniferous woodlands, from the point of view of their effects on other decomposer organisms.

No quantitative records exist on the rate at which invertebrates colonize decomposing leaves. Invasion of *Juncus* (wiregrass) leaves may be slow, but it does take place within 60 days of deposition on the soil surface. There is considerable scope for detailed observations on the manner in which soil invertebrates find and settle on plant materials.

The Biomass of Invertebrates in the Decomposer System

Modern studies illustrate that no single method exists for obtaining reliable estimates of the number of invertebrates in litter and soil. The only satisfactory procedure is to treat each major taxonomic group as an entity, developing a technique for that particular group. Even then, one would be wrong to assume that the different species within a given group can be extracted with equal efficiency. Methods for obtaining population estimates are described in Kevan (35), Murphy (45), and Southwood (60). Reference should be made to the individual chapters in Burges and Raw (12), and Macfadyen (40), who considers the principles and practical problems involved in sampling soil arthropods. The International Biological Program, with the cooperation of UNESCO, is producing a handbook on methods for soil biology (55).

Most methods of extracting invertebrates depend on the ability of the organisms to move along a particular gradient. These methods can have a high degree of extraction efficiency; however, their efficiency is affected by the condition of the organisms and, in particular, by differences in their capacity to react to changes in the enviromental gradients that are employed in the techniques. Ideally, extraction techniques should be independent of the organism's reactions, but such techniques have proved to be very laborious and, in many cases, they have not been any more efficient than the supposedly less desirable methods.

Considerable attention has been given to the extraction of small arthropods from litter and soil. Most of the methods which are used are modifications of the Tullgren funnel technique. Macfadyen (39) has improved the technique by steepening the temperature gradient and introducing a humidity gradient. The resulting "High Gradient" extractor possesses a high degree of efficiency for Collembola, and Block (5) found it 76 percent efficient for Acarina.

Salt et al. (57) introduced extensive improvements to mechanical methods by combining flotation with a technique for separating plant and insect materials based on their very different wetting properties. The method is highly efficient for soils with a high mineral content, but many arthropods intimately attached to coarse fragments of vegetation can escape extraction; the method, therefore, is not suitable for coarse litter. It has, however, provided an overall picture of the abundance of many diverse arthropod groups.

A new principle for mechanical sorting has been introduced by Aucamp and Ryke (2) and Aucamp (1). Their method depends on the fact that organisms adhere to plates covered with a grease film. Results so far indicate that this sorting method is much more efficient for oribatid mites than is the Tullgren-type extractor. It has not been tested for forest soils, and it seems likely that the coarse litter of coniferous soils will markedly reduce its efficiency, partly because the material may remove the grease film, and partly because some organisms will remain attached to portions of vegetation.

Our limited knowledge of soil organisms is exposed when we seek information on the total soil fauna and flora of any ecosystem. The only comprehensive figures given in Burges and Raw (12) are from Bornebusch (8); and Macfadyen (41) presents data for a "hypothetical grassland community." If we limit the study to arthropods, reliable information is available for a few sites. Salt et al. (57), for example, extracted 306,000 organisms per square meter, belonging to 19 orders of arthropods, from a cool-temperate grassland.

Table I gives biomass data for Macfadyen's hypothetical example and for four European localities. Some of the individual values must be treated with caution, particularly the figures from Stockli (61) which have been discussed by Nielsen (47) and Cragg (14). From the standpoint of soil biology, these figures represent a first attempt to present both the plant and animal components of the soil. The compilation is for Swiss meadowlands to a depth of 15 centimeters. The estimates of microflora, however, were derived from figures obtained at Rothamsted, England. Furthermore, in the light of other studies on lumbricid populations (See Table 6, Satchell, 58), it is unlikely that the Stockli estimate of 400 grams per square meter is typical for Swiss grasslands. A value not greater than 120 g/m^2 would seem more reasonable.

The Bornebusch examples provide a comparison between a deciduous mull and a *Picea* mor. We now believe that he underestimated some groups, and Cragg (14) attempted to provide revised figures.

The *Juncus* (wiregrass) site, on upland moorland in northern England, is similar in some ways to coniferous-bearing soils. The various organisms were extracted by methods specifically designed for the different taxonomic groups. Furthermore, each group was studied at regular intervals over at least one year, in order to allow for seasonal fluctuations. Latter and Cragg (38) investigated the microflora of the same site, and Heal (personal communication) has estimated the Protozoa. Thus, the figures for *Juncus* mor provide information on the major elements in the soil fauna and flora for one site, although not all the information was obtained over the same period of time.

The examples in Table 1 demonstrate a marked distinction be-

TABLE 1. Comparison of standing crop in g/m^2 (live wt.) for five European localities.

Organisms	Grassland (Stockli, 61)	(Macfadyen, 41)	Quercus Mull (Bornebusch, 9)	Revised Cragg, 14)	Picea—Raw Humus (Bornebusch, 9)	Revised Cragg, 14)	Juncus moor (Cragg, 9) (Latter & Cragg, 38)
Bacteria	2022	1000.0					135 *
Microfungi	2022	400.0					62 *
Protozoa	38	38.0					10.0*
Nematoda	5	12.0		2.5		4.5	1.6
Enchytraeidae	1.5	12.0	0.68	5.9	0.05	25.0	53.0
Lumbricidae	400	120.0	61.00	61.0	1.55	1.6	1.0
Collembola	81	5.0	0.10	5.2	0.14	6.8	0.1
Acarina	81	3.0	0.06	0.6	0.45	4.5	0.6
Gastropoda	81	10.0	5.32	14.9		7.6	
Isopoda	81	5.0	0.28	14.9		7.6	
Diplopoda	81	12.5	4.70	14.9		7.6	
Diptera	81	1.0	3.10	14.9	1.03	7.6	21.7†
Other insects	81	1.0	0.90	14.9	4.79	7.6	
Other invertebrates	81	7.4	0.67	14.9	1.83	7.6	
Total animals	525.5	225.9	76.81	90.1	9.84	50.0	88.0
Total microflora	2022.0	1400.0					197.0

The basis for the revised figures for the two Bornebusch sites is given in Table 9, Cragg (14).

*Denotes the highest estimates for microflora and protozoa given in Table 2, Latter & Cragg (38).

†Larvae of Tipulidae (Diptera).

tween the soil inhabitants of mor and mull sites. The two mor sites (*Picea* and *Juncus*), have very few large lumbricids. Their scarcity limits the amount of mechanical mixing of the litter and soil layers, allowing the accumulation of mor-type organic matter as a distinct horizon. This does not mean that their absence is responsible for the formation of mor humus. This, as Satchell (58) points out, results from the chemical nature of the forest litter.

The invertebrate fauna of mor soils is essentially a microfauna with enchytraeids, rarely longer than one to two centimeters, as the largest members. They constituted some 60 percent of the total biomass of the *Juncus* site and, in view of their abundance in soils with a high organic content, they probably dominate the soil and litter fauna in all coniferous habitats. Studies now in progress (Dash and Cragg, 16) in the Rockies suggest that their standing crop will not exceed one-fourth to one-third of the mean density 134,300/m^2 (live wt. 10.8 g) recorded by O'Connor (51) for a *Pseudotsuga menziesii* stand in north Wales.

If the preliminary results of Dash and Cragg (16) are indicative of the general abundance of the soil fauna in Rocky Mountain forests, then the total microfauna is unlikely to exceed the 88g/m^2 (wet wt.) recorded for *Juncus* moor. The average standing crop of microfauna on that site is interestingly enough equivalent to eight to ten hill sheep per acre. Because *Juncus* moor rarely carries more than two sheep per acre, and then only for approximately half the year, the soil and litter fauna is some four to five times the weight of the sheep grazing the vegetation.

Metabolic Aspects of the Decomposer System

The litter and soil communities process a large amount of organic material, and the extensive range of organisms involved, from the million or so bacteria per gram of soil to the many thousands of invertebrates, indicates that the processes of decomposition are both numerous and complex. To understand the working of a forest ecosystem at the decomposer level, we require information of two kinds: detailed information on the metabolic requirements of individual species and information on the transfer of energy through the various trophic levels.

Feeding Biology

We can make a few generalizations about soil invertebrates. Modern work shows that the major groups associated with coniferous forest soils are essentially grazers on the microflora. The protozoa are predominantly bacterial feeders (Stout and Heal, 62), and some species can certainly select specific bacteria. It is unlikely that they consume microfungi to any extent (Heal, 25). The nematodes show a great degree of variety in feeding habits. In more soils (Nielsen, 47, 50; Banage, 3) the majority feed on plant juices or bacteria, but some are important predators on Protozoa and other nematodes. The Enchytraeidae are mainly fungal feeders, and this is certainly the case for the species found by O'Connor (51) in a *Pseudotsuga* (fir) plantation. The Lumbricidae are well-known as plant feeders, but as Satchell (58) indicates, some species take in considerable amounts of soil, feeding on its microfloral protoplasm. The Collembola feed largely on microfungi. The Acarina show a range of food habits; many are important predators on other Acarina and on the microfauna in general. The Cryptostigmata, which are the most abundant Acarina in coniferous soils (Wallwork, 64), are both microfungal and bacterial feeders; some will feed on plant detritus and the faeces of other soil animals. Experiments have demonstrated that lumbricids can select their food materials. Bornebusch (9) lists the order of preference shown by *Lumbricus terrestris* (earthworm) for the leaves of a number of plant species. The gymnosperms are among those least preferred. *Abies alba* (silver fir) and *Pseudotsuga menziesii* (Douglas-fir) are ranked higher than *Pinus sylvestris* (Scotch pine), while the least palatable forms were *Picea abies* (Norway spruce), *Larix decidua* (European larch) and *L. leptolepis*. One of the major factors influencing palatability appears to be the polyphenolic compounds. Brown, Love, and Handley (11) have demonstrated their presence in the least palatable litters, whereas preferred materials such as *Mecurialis* and *Fraxinus* are free from such substances. Satchell (58), who reviews this important subject of palatability, has demonstrated the degree to which *L. terrestris* (earthworm) is repelled by different concentrations of catechin, a polyphenol present in many leaves.

Inter-relations of microfauna and microflora

The summary of feeding habits implies that the soil fauna, and certainly the microfauna characteristic of mor soils, plays no obvious part in the primary decomposition of plant tissue. Nielsen (49) studied the enzymes present in some 34 litter and soil invertebrates, which included enchytraeids, lumbricids, a wide range of arthropods (Acarina and Collembola were not investigated) and gastropods. He concluded that these invertebrates were not responsible for the very important first step in decomposition, namely, the transformation of the complex structural polysaccharides into assimilable monosaccharides. This first step is regarded as a major role of the microflora, although some Protozoa may be involved. Thus it seems likely that the abundant litter and soil invertebrates provide none of the biochemical machinery necessary for primary decomposition. However, their enzymes allow them to utilize the resultant products. That they are of importance is shown by the fact that the rate of decomposition of tree litter is negligible when they are absent.

The majority of the litter and soil invertebrates consume large amounts of plant material and produce copious faeces, the bulk of which is usually undigested plant fragments. These materials are dispersed throughout the litter and soil and, in theory, provide a wide range of different substrates for microorganisms. Whether invertebrate faeces do provide such substrates still remains undecided. Witkamp and van der Drift (65) concluded that the faecal pellets of *Enoicyla pusilla* (Tricoptera) larvae, which live in litter, are a more favorable habitat for microorganisms than is whole leaf litter. On the other hand, Nicholson, Bocock, and Heal (46) studying the breakdown of the faeces of *Glomeris*, a characteristic millipede in many soils, concluded that their rate of breakdown was no greater than that of fresh litter. However, even if faeces, in some cases, are not more suitable for microbial attack than is the surrounding litter, the mechanical transportation of microorganisms may be of considerable importance. Discussing lumbricids, which have been studied extensively, Satchell (58) ends his review with the following sentence: "On present evidence, conditioning plant remains for microbial decomposition seems to be the most important action of Lumbricidae in the ecosystem."

The microflora are the main agents in the decomposition process; at the same time, they serve as the main food supply for many members of the microfauna. At first sight, these two roles appear to be in conflict, and it might seem that the microfauna could limit the decomposer activities of the microflora. However, the results of exclusion experiments using nylon nets demonstrate that, where members of the microfauna are excluded, the rate of decomposition is reduced. Thus, there must be an important interaction between the two components of the soil community. The mechanical role of the fauna in subdividing plant tissues provides a greater surface area for the operation of the microflora. Furthermore, the microfauna can act as agents of dispersal for the microflora. Macfadyen (43) suggests the important possibility that the grazing activity of the microfauna prevents the ~~develop~~ment the grazing activity of the microflora. It may be that by preventing aging, the fauna maintains a high level of activity in the microflora.

Metabolism of litter and soil populations

Macfadyen (43) has attempted to analyse the roles of the herbivore, decomposer, and predator trophic levels in nine soil communities. His sites include four of those listed in Table I, and his comparison of the total annual respiration contributed by each of the trophic levels in these four sites is shown in Figure 4. There are clear distinctions between mor and mull sites, the former, which includes coniferous forest, shows a high metabolic output on the part of the small decomposers which comprise Collembola, Enchytraeidae, some 50 percent of the Nematoda and the oribatid Acarina. The Protozoa were not included in the analysis. Macfadyen also draws attention to the fact that in all nine sites the contribution of the herbivore trophic level was remarkably uniform. Engelmann (21), using the Macfadyen data, also comments

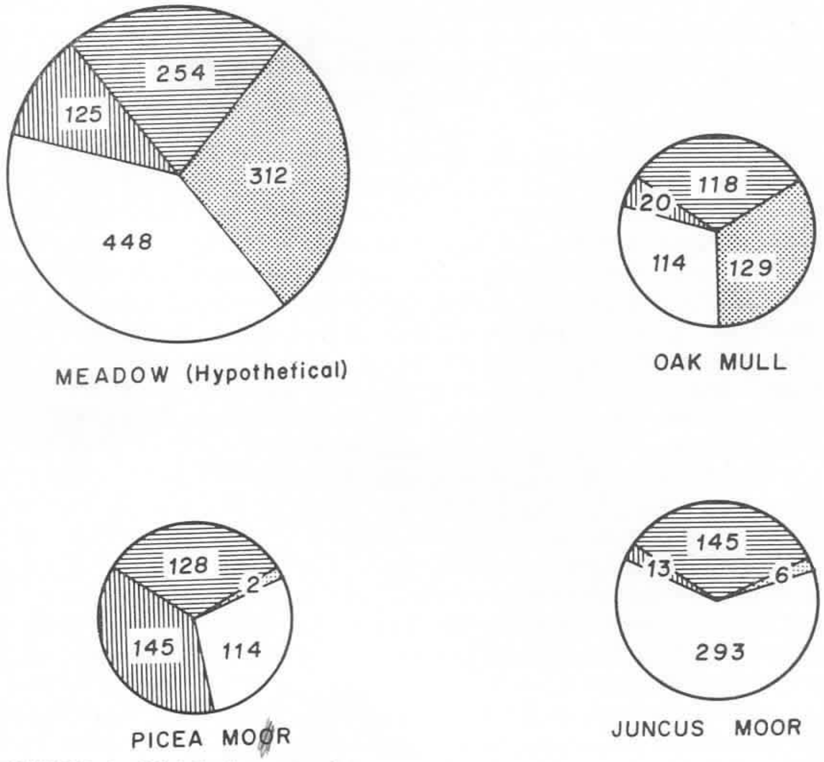


FIGURE 4. Metabolism of Different Trophic Levels. Comparison of the total annual respiration of four sites. Sectors reading clockwise from the top represent herbivores, large decomposers, small decomposers, and predators.

on the similarity in herbivore metabolism, which amounted to some 20 to 33 percent of the total metabolism for each community.

This analysis represents no more than a superficial attempt to arrive at a model for the overall metabolism of a decomposer system. On the basis of our present knowledge, it is difficult to assign organisms to particular trophic levels. In fact, if we are to derive a meaningful picture of the processes in the decomposer system, we will have to erect a model of microlevels with which we can study biochemical details based on nutritional requirements. Although there is a shortage of such information, this field of enquiry is currently attracting attention, as Burges and Raw (12) show.

Before we can prepare a worthwhile balance sheet of the metabolic operations in a community, we must have a reliable measure of how much new protoplasm is produced for each group of organisms involved in the community. Table I is concerned with average standing crops. For realistic assessments of production, that is, the amount of organic matter produced in a specified time interval (irrespective of whether or not it survives to the end of that interval), the standing crop is not sufficient. We must know the population density, age and sex structure, food assimilation, and respiration of the dominant organisms. At present, we have few complete investigations.

If we compare the results of studies made by Engelmann (20) with those made by Berthet (4) on Acarina, those of Healey (26, 27) on Collembola with those of Nielsen (48) on Nematoda, and those of Nielsen (48) with those of O'Connor (52) on Enchytraeidae, we can see that the metabolic activity of the Nematoda and Enchytraeidae outweights that of the micro-arthropods by a factor of 10 to 20. Macfadyen (43) suggests that the soil fauna is responsible for not more than 20 percent of the total metabolic activity of the soil community. In view of the high rates found for nematode and enchytraeid populations, the microfauna may account for much more than 20 percent in coniferous forest soils.

Conclusion

This sketch of the composition and role of the invertebrate fauna of litter and soil exposes our present ignorance of what constitutes a range of animal communities of considerable size, both in terms of abundance of organisms and in terms of variety of taxonomic groups. Some of the missing information will come out of various International Biological Program projects. I stress the need for taxonomic studies, because without a sound taxonomy the study of many aspects of soil biology becomes meaningless. We require census data for all soil invertebrates present in the same site. We also need to know more about the general biology of a number of relatively common soil organisms in order to form a basis for detailed investigations on the metabolic activities of soil organisms in general.

Although such studies should be planned within a systems approach (Van Dyne, 63), an approach that is being emphasized in many International Biological Program studies, particularly in the United States, I cannot overemphasize the need for the careful collection of basic biological information in the field. There has been a tendency in soil biology to seek quantitative information on activity and gross distribution, to the neglect of observational studies on micro-distribution. For example, while Darwin and others have emphasized the importance of lumbricids in soil formation, the part played by the microfauna was overlooked. According to Kubiena (36), the A_1 and A_2 horizons of the Pitchrendzina of the Austrian Alps are coprogenous in origin and made up of collembolan faeces to a depth of some 30 centimeters. Zachariae (66, 67, 68) has examined the form and distribution of invertebrate faeces in many soils. He concludes that the so-called collembolan soils have been formed by Enchytraeidae. His studies on the distribution of faeces, in relation to different litter and soil horizons, deserve attention.

Zachariae's studies are typical of the current developments in soil micro-morphology. Jongerius (31) has developed soil sectioning techniques that allow for a detailed study of different forms of humus. With the introduction of the ~~Electr~~oscan microscope, it has become possible to "see" the distribution of bacterial colonies on soil particles, and with further refinements the microscope should provide much needed detail on the micro-habitats within which the soil microorganisms and invertebrates operate.

The functioning of a natural ecosystem depends upon the efficient operation of its decomposer component. Now that so many of man's activities affect ecosystems, we need to understand how they operate and how units within them are influenced by various types of interference. Even if our present knowledge of decomposer processes is largely fragmentary, we know what happens when some of the organisms are put out of action. Raw (56), for example, has described changes in the soil profile of an apple orchard where copper sulphate had killed the lumbricids. Karg (32) has demonstrated the selective effect of certain persistent insecticides on field populations of Collembola and Acarina. Some species were reduced to low levels or completely destroyed, whereas others reached high densities. In some cases, the final result was to accelerate the rate of decomposition.

Literature Cited

1. Aucamp, J. L. 1967. Efficiency of the grease film extraction technique in soil micro-arthropod surveys. Pp. 515-523. *In* O. Graff and J. E. Satchell (eds.) Progress in soil biology. North-Holland Publishing Co., Amsterdam.
2. Aucamp, J. L. and P. A. J. Ryke. 1964. A preliminary report on a grease film extraction method for soil micro-arthropods. Pedobiologia 4:77-79.
3. Banage, W. B. 1963. The ecological importance of free-living soil nematodes with special reference to those of moorland soil. J. Anim. Ecol. 32:133-140.
4. Berthet, P. 1967. The metabolic activity of oribatid mites (*Acarina*) in different forest floors. Pp. 709-725. *In* K. Petrusewicz (ed.) Secondary productivity of terrestrial ecosystems. Vol. II.
5. Block, W. 1966. Some characteristics of the Macfadyen high gradient extractor for soil micro-arthropods. Oikos 17:1-9.
6. Bocock, K. L., and O. Gilbert. 1957. The disappearance of leaf litter under different woodland conditions. Plant and Soil. 9:179-185.
7. Bocock, K. L., O. Gilbert, C. K. Capstick, D. C. Twinn, J. S. Waid, and M. J. Woodman. 1960. Changes in leaf litter when placed on the surface of soils with constrasting humus types. J. Soil Science 11:1-9.
8. Bornebusch, C. H. 1930. The fauna of forest soil. Nielsen and Lydiche, Copenhagen. 224 pp.
9. Bornebusch, C. H. 1953. Laboratory experiments in the biology of earthworms. Dansk. Skovoforen. Tidsskr. 38:557-579.
10. Bray, R. J., and E. Gorham. 1964. Litter production in forests of the world. Pp. 101-157. *In* Advances in ecological research Vol. II. Academic Press, London and New York.
11. Brown, B. R., C. W. Love, and W. R. C. Handley. 1963. Rep. Forest Res. London, 1922. Pp. 90-93.
12. Burges, A., and F. Raw (eds.). 1967. Soil biology. 532 pp. Academic Press, London and New York.
13. Carlisle, A., A. H. F. Brown, and E. J. White. 1966. The organic matter and nutrient elements in the precipitation beneath a sessile oak (*Quercus petrae*) canopy. J. Ecol. 54:87-98.
14. Cragg, J. B. 1961. Some aspects of the ecology of moorland animals. J. Ecol. 49:477-506.
15. Darwin, C. R. 1881. The formation of vegetable mould through the action of worms, with observation on their habits. Murray, London.
16. Dash, M. C., and J. B. Cragg. 1968. Unpublished.
17. Doeksen, J., and van der Drift (eds.). 1963. Soil organisms VIII. 453 pp. North-Holland Publishing Co., Amsterdam.
18. Douglas, L. A., and J. C. F. Tedrow. 1959. Organic matter decomposition rates in arctic soils. Soil sci. 88:305-312.
19. Edwards, C. A., and G. W. Heath. 1963. The role of soil animals in breakdown of leaf material, pp. 76-84. *In* J. Doeksen and J. van der Drift [eds.] Soil organisms. North-Holland Publishing Co., Amsterdam.
20. Engelmann, M. D. 1961. The role of soil arthropods in the energetics of an old-field community. Ecol. Monographs 31:221-238.

21. Engelmann, M. D. 1968. The role of soil arthropods in community energetics. Amer. Zoologist 8:61-69.
22. Graff, O., and J. E. Satchell [eds.] 1967. Progress in soil biology. North-Holland Publishing Co., Amsterdam. 656 pp.
23. Hayes, A. J. 1964. Biology of forest soils: Mycology of Scots pine litter. Report on Forest Research, Mar. 1964:101-110. H.M.S.O., London.
24. Hayes, A. J. 1965. Some microfungi from Scots pine litter. Brit. Mycol. Soc., Trans. 48(2):179-185.
25. Heal, O. W. 1963. Soil fungi as food for amoebae, pp. 289-297. *In* J. Doeksen and J. van der Drift [eds.] Soil organisms. North-Holland Publishing Co., Amsterdam.
26. Healey, I. N. 1967a. The population metabolism of *Onychiurus procampatus* Gisin (Collembola), pp. 127-134. *In* O. Graff and J. E. Satchell [eds.] Progress in soil biology. North-Holland Publishing Co., Amsterdam.
27. Healey, I. N. 1967b. The energy flow through a population of soil *Collembola*, pp. 695-704. *In* K. Petrosewicz [ed.] Secondary productivity of terrestrial ecosystems Vol. II. Institute of Ecology, Polish Academy of Sciences, Warsaw.
28. Jacot, A. P. 1936. Soil structure and soil biology. Ecology 17:359-379.
29. Jacot, A. P. 1939. Reduction of spruce and fir litter by minute animals. J. For. 37:858-860.
30. Jacot, A. P. 1940. The fauna of the soil. Quart. Rev. Biol. 15:28-58.
31. Jongerius, A. 1963. Optic-volumetric measurements on some humus forms, pp. 137-148. *In* J. Doeksen and J. van der Drift [eds.] Soil organisms. North-Holland Publishing Co., Amsterdam.
32. Karg, W. 1967. Veränderungen in den Bodenlebensgemeinschaften durch die Einwirkung von Pflanzenschutzmitteln, pp. 310-319. *In* O. Graff and J. E. Satchell [eds.] Progress in soil biology. North-Holland Publishing Co., Amsterdam.
33. Kendrick, W. B. 1959. The time factor in the decomposition of coniferous leaf litter. Can. J. Bot. 37:907-912.
34. Kendrick, W. B., and A. Burges. 1962. Biological aspects of the decay of *Pinus sylvestris* leaf litter. Nova Hedwigia 4:313-342.
35. Kevan, D. K. McE. 1962. Soil animals. Witherby, London. 237 pp.
36. Kubiena, W. L. 1953. The soils of Europe. London. 316 pp.
37. Kühnelt, W. 1961. Soil biology. Faber and Faber, London. 399 pp.
38. Latter, P., and J. B. Cragg. 1967. The decomposition of *Juncus squarrosus* leaves and microbiological changes in the profile of *Juncus* moor. J. Ecol. 55:465-482.
39. Macfadyen, A. 1961. Improved funnel-type extractor for soil arthropods. J. Anim. Ecol. 30:171-184.
40. Macfadyen, A. 1962. Soil arthropod sampling. Pp. 1-34. *In* Advances in ecological research Vol. I. Academic Press, London and New York.
41. Macfadyen, A. 1963a. Animal ecology, aims and methods. Pitman Ltd., London. 344 pp.
42. Macfadyen A. 1963b. Energy flow in ecosystems and its exploitation by grazing, pp. 3-20. *In* D. J. Crisp [ed.] Grazing in terrestrial and marine environments. Blackwell Scientific Publications, Oxford, England.

43. Macfadyen, A. 1963c. The contribution of the microfauna to total soil metabolism. pp. 3-16. *In* J. Doeksen and J. van der Drift [eds.] Soil organisms. North-Holland Publishing Co., Amsterdam.
44. Müller, P. E. 1878. Studier over Skavjord. I Om Bogenmuld og Bogemor paa Sand og Ler. Tidsskrift for Skovbrug, Vol. 3, 1879.
45. Murphy, P. W. [ed.] 1962. Progress in soil zoology. Butterworths, London. 398 pp.
46. Nicholson, P. B., K. L. Bocock, and O. W. Heal. 1966. Studies on the decomposition of the faecal pellets of a millipede (*Glomeris marginata* (Villiers). J. Ecol. 54:755-766.
47. Nielsen, C. O. 1949. Studies on the soil microfauna 2. The soil inhabiting nematodes. Natura Jutl. 2:1-131.
48. Nielsen, C. O. 1961. Respiratory metabolism of some populations of enchytraeid worms and free living nematodes. Oikos 12:17-35.
49. Nielsen, C. O. 1962. Carbohydrates in soil and litter invertebrates. Oikos 13, II:200-215.
50. Nielsen, C. O. 1967. Nematoda, pp. 197-211. *In* A. Burges and F. Raw [eds.] Soil biology. Academic Press, London and New York.
51. O'Connor, F. B. 1957. An ecological study of the enchytraeid worm population of a coniferous forest soil. Oikos 8, II:161-199.
52. O'Connor, F. B. 1963. Oxygen consumption and population metabolism in Enchytraeidae, pp. 32-48. *In* J. Doeksen and J. van der Drift [eds.] Soil organisms. North-Holland Publishing Co., Amsterdam.
53. Ovington, J. D. 1962. Quantitative ecology and the woodland ecosystem concept, pp. 103-197. *In* Advances in ecological research Vol. 1. Academic Press, London and New York.
54. Petrusewicz, K. [ed.] 1967. I.B.P. handbook: secondary productivity of terrestrial ecosystems. Institute of Ecology, Polish Academy of Sciences, Warsaw. 2 vols.
55. Phillipson, J. 1969. I.B.P. handbook: methods of study in quantitative soil ecology. (In preparation.)
56. Raw, F. 1962. The effect of orchard management on earthworm populations. Rep. Rothamst. Exp. Sta. p. 158.
57. Salt, G., F. S. K. Hollick, F. Raw, and M. V. Brian. 1948. The Arthropod population of pasture soil. J. Anim. Ecol. 17:139-150.
58. Satchell, J. E. 1967. Lumbricidae, pp. 259-322. *In* A. Burges and F. Raw [eds.] Soil biology. Academic Press, London and New York.
59. Shanks, R. E., and J. S. Olson. 1961. First year breakdown of leaf litter in southern Appalachian forests. Science N.Y. 134:194-195.
60. Southwood, T.R.E. 1966. Ecological methods. Methuen & Co. Ltd., London. 391 pp.
61. Stöckli, A. 1946. Der Boden als Lebensraum. Viertelj. schr. Naturf. Ges. Zurich 91.
62. Stout, J. D., and O. W. Heal. 1967. Protozoa, pp. 150-195. *In* A. Burges and F. Raw [eds.] Soil biology. Academic Press, London and New York.
63. Van Dyne, G. M. 1966. Ecosystems, systems ecology and systems ecologists. U.S. Atomic Energy Comm. Pub. 161. Oak Ridge Nat. Lab., Tenn.
64. Wallwork, J. A. 1967. Acari, pp. 363-395. *In* A. Burges and F. Raw [eds.] Soil biology. Academic Press, London and New York.

65. Witkamp, M. T., and J. van der Drift. 1959. The significance of the breakdown of oak litter by *Enoicyla pusilla*. Burm. Arch. Néerl. de Zool. 13:486-492.

66. Zachariae, G. 1963. Was leisten Collembolen för den Waldhumus? pp. 109-123. *In* J. Doeksen and J. van der Drift [eds.] Soil organisms. North-Holland Publishing Co., Amsterdam.

67. Zachariae, G. 1964. Welche bedeutung haben Enchytraeen im Waldboden? pp. 57-68. *In* A. Jongerius [ed.] Soil micromorphology. Elsevier Publishing Co., Amsterdam.

68. Zachariae, G. 1965. Spuren tierischer Tätigheit im Boden des Buchenwaldes. Heft 20. Paul Parey, Hamburg and Berlin. 68 pp.

Discussion

Question: Is most of the soil microfauna within one or two centimeters of surface, or are there appreciable numbers at lower levels?

Dr. Cragg: Most of the microfauna is confined to the upper layers of the A horizon and to the zone which I usually describe as the fermentation layer. The organisms in which I am particularly interested, the nematodes, protozoa, enchytraeids, collembola and mites, occur abundantly in the region of the fermentation zone. In coniferous soils, because strong burrowing forms are absent, most of the fauna is confined to the top six inches of the litter and soil complex.

Question: Some of our forest types in the Northern Rockies are susceptible to very intensive fires, which appear to consume practically all the soil above the mineral surface. How do the micro-organisms survive?

Dr. Cragg: Most of them have remarkable recovery powers, as do many other invertebrates. There will be a spell when they are perhaps not numerous, but they do recover quite well after forest fires. But first you must reestablish the food material, which in most cases is the microflora.

Question: Then the microfauna would have to survive essentially in the mineral soil?

Dr. Cragg: Yes, but there will be pockets of soil with some organic material in it which will act as refuges or reservoirs for these organisms.

Someone mentioned the rapid accumulation of litter in some situations. This is important, because it shows that the decomposer processes are working very slowly indeed. I am reminded of an example. In Australia there are plantations of *Pinus radiatoa,* where there are virtually no litter organisms at work, and where, as a consequence, the litter is piling up and there is poor recirculation of nutrients. The second crop of *radiata* is some 20-25 percent below the first crop.

Question: Are there differences between the soil microfaunas in different plant communities: grassland, deciduous forest, coniferous forest, and so on?

Dr. Cragg: Yes. There are various differences in composition. In Europe, one of the major differences is that in grasslands and in deciduous woodlands, the earthworms play a very large part. In coniferous forest, you have no earthworms, and this, of course is one of the reasons why most activity within the soil is very close to the surface.